Selection for Early Heading and Correlated Response in Maturity of Soft Red Winter Wheat

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ABSTRACT

Heading date in wheat (*Triticum aestivum* L. emend. Thell.) is an easily identifiable trait, and previous research has shown it can be modified. However, several studies have shown that heading date is not always highly correlated with harvest maturity. This study was conducted to gain a more thorough understanding of the relationships between heading date and traits related to maturity such as kernel growth rate (KGR), effective filling period (EFP), and time of physiological maturity. We evaluated direct and correlated response to two cycles of phenotypic recurrent selection for early heading date in two wheat populations in 1989. Direct response to selection for early heading date was −5 and −10 d, respectively, in the two populations. In Population 1, correlated response to selection was not significant. We observed a significant reduction in mean KGR from 2.56 to 2.13 mg kernel^{-1} d^{-1} from the C_0 to the C_2 in Population 2, with no significant change in mean EFP. Heritability estimates ranged from 0.10 for yield in population 1 to 0.81 ($P<0.01$) for heading date in Population 2. Mean estimated date of physiological maturity (EPM) was significantly reduced in both populations after two selection cycles. Early EPM of the C_2 apparently reflected an early heading date and not a reduced grain filling period. However, the earliest heading entries were not always the first to reach EPM. Thus we suggest a maturity rating based on EPM in later generations to ensure continued selection pressure for early physiological maturity.

THE PRACTICE of doublecropping soybean [*Glycine max* (L.) Merr.] with small grain has necessitated development of earlier-maturing wheat cultivars. In Kentucky, ≈95% of the wheat is grown in a doublecrop system with soybean as the second crop. An early wheat harvest improves the chances of obtaining a good stand of soybean, particularly under conditions of summer drought. In addition, late plantings of photoperiod-sensitive soybean cultivars may result in shorter plants with reduced yields (Egli, 1976; Norman, 1978).

Heading date in wheat is an easily identifiable character that can be modified through selection (Allard and Harding, 1963; Avey et al., 1982; Frederickson and Kronstad, 1985). However, as Florell (1924) and Van Sanford (1985) noted, heading date is not always an accurate measure of maturity in wheat. Florell (1924) found that varieties that headed first did not necessarily mature first. He noted that the time between appearance of the first few heads and full headed condition was generally greater than the time between ripening of the first few plants and ripening of the whole plot. He further stated that ripening is often abnormal due to the environment. More recently, Van Sanford (1985) found that two entries in the Uniform Southern Soft Red Winter Wheat Nursery flowered 8 d apart yet reached physiological maturity at approximately the same time. He concluded that selection for early anthesis and high yield might produce genotypes that reach physiological maturity later than those that flower late.

Maturity in seed crops consists of two components: physiological maturity, defined as time of maximum seed dry weight (Shaw and Loomis, 1950), and harvest maturity, defined as the point at which seed moisture concentration is sufficiently low that the seed may be harvested and safely stored. Selection for harvest maturity is difficult, since the period between physiological maturity and harvest maturity involves moisture loss from the seed, which can be strongly affected by the environment (Clarke, 1983). Selection for time of physiological maturity in wheat is also difficult. Accurate visual indicators of physiological maturity similar to black layer in corn (*Zea mays* L.) (Daynard and Duncan, 1969), a black pigment in the pericarp of barley (*Hordeum vulgare* L.) (Harlan, 1923) and a dark closing layer in the placental area near the sorghum [*Sorghum bicolor* (L.) Moench] kernel attachment point (Eastin et al., 1973) are lacking in wheat. Plant characteristics such as the complete loss of green color from the glumes (Hanft and Wyche, 1982; Singh et al., 1984) have been proposed, but can be subjective and difficult to assess in the presence of glume blotch [*Stagonospora nodorum* (Berk.) Cast. & Germ.] as well as in genotypes with bronze chaff.

The time between anthesis and physiological maturity in wheat is a function of the rate and duration of kernel growth. It has been suggested that selection for high kernel growth rate and short filling period might be appropriate to develop earlier maturing genotypes (Nass and Reiser, 1975; Van Sanford, 1985; Bruckner and Frohberg, 1987). Unfortunately, these traits are difficult and expensive to measure on the large numbers of genotypes typically evaluated in wheat breeding programs. Although heading date is amenable to selection, its effect on time of physiological maturity has not been evaluated. We conducted this study to (i) examine the effect of selecting for early heading date on length of the post-anthesis development period in wheat; and (ii) estimate genetic correlations among and heritability of traits related to maturity, such as kernel growth rate and effective filling period (Daynard et al., 1971).

MATERIALS AND METHODS

Selection studies were initiated in the spring of 1987 in two populations. Population 1 was the F_2 generation of the cross Florida 7927-G14/NASW-78-171. Population 2 was a synthetic known as the dynamic gene pool, representing a collection of genotypes from several breeding programs that were intermated for several cycles in a cooperative

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Abbreviations: ANOVA, analysis of variance; C_n, the nth cycle; C_1–S, C_1 selected; DAA, days after anthesis; EFP, effective filling period; EPM, estimated date of physiological maturity; KGR, kernel growth rate; MDT, mean daily temperature.

regional project. The populations were planted at Spindletop Farm, near Lexington, KY, on 24 Oct. 1986 in six-row plots 3 m in length with 18-cm row spacing, at an approximate seeding rate of 4.5 g m^{-2}. Heading date for an individual plant was defined as the day of complete spike emergence from the flag leaf sheath. In Population 1, 40 plants which headed earliest were selected and intermated by pair crosses. In Population 2, 90 plants which headed earliest were selected and intermated by pair crosses. In each population, 50% of the selections were designated as males and 50% as females. The exact selection intensity was unknown, since the number of plants in each population was not determined. At maturity, the crossed seed was harvested to form the cycle 1 (C_1). There were 20 successful crosses in Population 1 and 42 in Population 2.

For the second cycle of selection, 10 seeds per cross were bulked in each population. Crosses producing fewer than 10 seeds were discarded. In Population 1, 170 seeds were advanced, while in Population 2, 330 seeds were advanced. Seedlings were vernalized for 8 wk at 3 °C and transplanted to the greenhouse. The first 20% of the plants to head in each population were tagged and intermated by pair crosses. Seed from crosses was harvested to constitute the C_2.

To evaluate progress from selection in a replicated experiment it was necessary to increase seed quantities. The C_2 seedlings were vernalized as previously described, planted in the greenhouse, and selfed seed was harvested. Remnant C_1 seed was planted in unreplicated increase plots at Spindletop Farm on 30 Oct. 1987, and selfed seed was harvested from 100 plants to represent the C_1. Self-pollinated spikes of seed and pollen parents were also harvested and were planted as headrows at Spindletop farm on 30 Oct. 1987. Each row was bulk harvested. This seed, designated C_1 selected (C_1–S), represented selected individuals of the base population (C_0). To represent the unselected C_0, 100 random plants were harvested from each population and were planted as headrows at Spindletop Farm on 30 Oct. 1987. Each row was bulk-harvested at maturity to provide S_2 seed of the C_0.

The C_0, C_1, C_2, and C_1–S lines were planted at Spindletop Farm on 27 Oct. 1988. Selected and unselected lines from the C_0 were evaluated in the S_2 generation; lines from Cycles 1 and 2 were in the S_1 generation. The soil type was a Maury silt loam soil (fine, mixed, mesic Typic Paleudalf). The experimental design was a split-plot with cycles as main plots and entries in cycles as subplots. Main plots were arranged in randomized complete blocks with two replications. A variable number of entries represented each cycle. For example, in the most extreme case (Population 1) only 15 C_2 entries yielded sufficient seed for a replicated design, while the C_0, C_1–S, and C_1 were represented by 30 randomly drawn entries. The experimental unit was a two-row plot, 0.61 m wide and 0.61 m long, planted at a rate of 107 seeds m^{-2}. The experiment was bordered on all sides with rows of several check cultivars.

Ammonium nitrate was applied in split applications of 50 kg N ha^{-1} at Feekes growth stages 5 and 8 (Large, 1954). Weed control was accomplished with an application of thifensulfuron herbicide on 13 Apr. 1989 at 0.025 kg ha^{-1}. Powdery mildew (*Erysiphe graminis* f. sp. *tritici*) and *Septoria* diseases were controlled with applications of propiconazole fungicide at 0.035 kg ha^{-1} on 27 Apr. and 1 June 1989.

Response variables included heading date, determined when 50% of the spikes in the plot were completely emerged from the flag leaf sheath; anthesis date, determined when 50% of the spikes in a plot displayed extruded anthers; kernel growth rate; effective filling period; and an estimated date of physiological maturity, calculated as anthesis date + EFP. For the measurement of KGR, ≈12 spikes per plot were tagged at anthesis. Samples of three spikes were harvested at 20 DAA, and at harvest maturity. Spikes were threshed, and kernels were counted and dried at 65 °C for 48 h before weighing. The KGR was estimated as mean kernel dry wt. at 20 DAA/10 and expressed as mg $kernel^{-1}$ d^{-1}. This simplified method of measuring KGR was justified by May (1990), who demonstrated a high correlation (r = 0.80 to 0.90, $P < 0.01$) between KGR determined by this method and KGR determined from two kernel samples taken during the linear phase of kernel growth. The simplified method greatly reduces the required number of samples and consequently allows KGR to be estimated on a large number of genotypes. The EFP in days was calculated as final average kernel dry wt./KGR. Mean daily temperature was computed for the period between 10 and 20 DAA for each entry.

Design I matings (Comstock and Robinson, 1948) were completed in each wheat population using a subset of seed from the 100 plants representing the C_0. Sixty S_1 lines were divided into three sets of 20 rows during vegetative growth. Four rows per set were designated as males and 16 rows per set as females. Each male was mated to a different group of four females within each set. This procedure was carried out in the field and greenhouse; seed from each mating in the greenhouse was composited with seed from the corresponding mating in the field.

Design I progeny of each population were planted at Spindletop Farm on 27 Oct. 1988. The experimental design was a split-plot with sets as main plots and matings assigned to subplots. Main plots were arranged in randomized complete blocks with two replications. The experimental unit was a two-row plot 0.61 m long and 0.61 m wide planted at a rate of 94 seeds m^{-2}. The same traits described in the selection study were measured, as well as grain yield (g m^{-2}).

Statistical Analysis

All response variables were subjected to analysis of variance (ANOVA) in the selection study. Cycles were considered fixed while entries in cycles were considered random. There was no exact F-test for cycle differences; therefore, the appropriate combination of mean squares was synthesized. Numerator and denominator degrees of freedom were estimated by Satterthwaite's approximation (Satterthwaite, 1946). When significant differences existed among cycles, means were separated with a nonorthogonal, but meaningful, set of contrasts. However, when main plot error was not significant ($P > 0.25$), it was pooled with subplot error (Carmer et al., 1969) to provide an exact F-test for cycle differences. If significant differences existed among cycles, the means were separated with the LSD. Linear relationships among response variables were evaluated with simple correlation analysis of entry means.

In the ANOVA of the Design I progeny all sources of variation were considered random. In the case of balanced data, mating design variance components were estimated for sources of variation in the subplot analysis. In the case of missing observations, least-squares estimates of the missing observations were inserted into the data set. Subsequently, an ANOVA was run as if the data were balanced except that 1 df was subtracted from the subplot error term for each missing observation and the error mean square was recomputed.

Narrow-sense heritability was estimated on a paternal half-sib family-mean basis directly from the male (set) variance component and the male(set) mean square as described by Knapp et al. (1985). A 90% confidence interval according to Knapp et al. (1985) was formed for all estimates of heritability for which the male (set) F-test was significant at $P < 0.05$.

Additive genetic correlations (r_a) between traits were cal-

culated according to Mode and Robinson (1959). When σ_a could not be estimated due to a negative estimate of the male (set) variance component, a genetic correlation (r_g) was estimated from the female[male(set)] components of variance and covariance. The genetic correlation was not estimated when the male(set) component of variance was negative for one trait and the female[male(set)] component of variance was negative for another trait. Predicted direct and correlated response to selection was calculated after Falconer (1981).

RESULTS AND DISCUSSION

Mean heading date was significantly earlier after one cycle of mass selection with intermating in both wheat populations (Table 1) with gains of 4 and 7 d. After two cycles, mean heading date was ≈5 and 10 d earlier than the C_0 in Population 1 and 2, respectively. These results agree with other studies reporting response to selection for early heading date (Allard and Harding, 1963; Avey et al., 1982; Frederickson and Kronstand, 1985).

Greater progress for early heading date was made in the first cycle of selection than in the second. This has been noted in other studies (Avey et al., 1982; Frederickson and Kronstad, 1985). Avey et al. (1982) attributed greater response in Cycle 1 vs. Cycle 2 to selection for major genes affecting heading date in the first cycle and for minor genes in later cycles. Greater response in the first cycle of selection in our study could simply reflect a higher selection intensity. While selection intensity in the second cycle was known to be 20%, we estimated a selection intensity of 5% in the first cycle. It is also possible that in sampling the C_0 after the C_1–S plants had been harvested, we introduced a bias into the estimated difference between the C_0 and C_1. We estimated this bias to be quite small: ≈0.15 d in population 1 and 0.34 d in population 2.

A third factor that might explain greater response in the C_1 than the C_2 is that no pedigree information was recorded, and thus it is possible that we made crosses within the same family, which could have limited opportunities to accumulate different genes affecting heading date.

In population 1, we observed no significant correlated responses in KGR or EFP (Table 1). Mean EPM was 2.4 d earlier in the C_1 than in the C_0, but there was no significant change in mean EPM from the C_1 to the C_2. In the absence of change in EFP, it appears that earlier EPM of the C_1 compared to the C_0 reflects earlier heading date rather than shorter grain filling period.

In Population 2, mean KGR was reduced from 2.56 mg kernel^{-1} d^{-1} in the C_0 to 2.13 mg kernel^{-1} d^{-1} in the C_2 (Table 1). There was no significant difference in mean KGR between the C_1–S and the C_1. There is some difficulty in attributing the lower KGR of the C_2 entirely to correlated response to selection for early heading date. Given the widely reported temperature effects on KGR (Saunders, 1928; Sofield et al., 1977; Warrington et al., 1977; Pinthus and Sar-Shalom, 1978; Weigand and Cuellar, 1981; Van Sanford, 1985), the higher KGR of the C_0 could be due in part to later flowering, and hence kernel development under higher temperatures. However, MDT from 10 to 20 DAA and KGR were not highly correlated in any of the cycles or in the combined analysis of all cycles (data not shown). Additionally, MDT during the period 10 to 20 DAA for the late flowering C_0 was actually lower than MDT 10 to 20 DAA for the earlier flowering C_1 or C_2 (data not shown). Thus, the data do not support the hypothesis that high KGR in the C_0 in Population 2 was related to temperature.

Selection in Population 2 did not bring about a change in mean EFP (Table 1). Mean EPM, however, was ≈6 d earlier in the C_2 than in the C_0 (Table 2). As in Population 1, earlier mean EPM of the C_1 and C_2 was apparently due to an earlier heading date, since EFP was not altered by selection.

Results of this study indicate that time of physiological maturity may be modified simply by selecting for heading date. Van Sanford (1985) found several soft red winter wheat genotypes that headed up to 1 wk apart yet reached EPM at the same time. That trend is not evident in the cycle means of this study (Table 1). However, some C_1 lines in Population 2 headed on the same day but differed in EPM by almost 7 d (Table 2). We also found later-heading entries that reached EPM before some earlier-heading entries. These were exceptions to the high correlation between heading date and EPM calculated from all entries and cycles in both populations (Table 3).

In the ANOVA of Design I progeny, significant

Table 1. Direct and correlated response to selection for early heading date (HD) in two wheat populations.

Population	Cycle	HD	EPM†	KGR	EFP
		— Day of year —		mg kernel^{-1}	d^{-1}
1	C_0	137.7a‡	155.3c	2.35a	14.0a
	C_1–S	134.7b	153.8b	2.39a	14.3a
	C_1	133.8b	152.9ab	2.31a	14.3a
	C_2	132.3c	152.1a	2.21a	14.1a
2	C_0	142.5a	158.3a	2.56a	12.8a
	C_1–S	136.5b	155.6b	2.33ab	14.8a
	C_1	135.7b	154.4b	2.34b	14.4a
	C_2	132.5c	152.5c	2.13c	14.6a

†EPM = estimated date of physiological maturity, KGR = kernel growth rate, EFP = effective filling period.
‡Means followed by same letter not significantly different at P≤0.05.

Table 2. Means and standard errors (SE) of heading date (HD), effective filling period (EFP) and the estimated date of physiological maturity (EPM) for several entries in wheat Population 2.

Cycle	Entry	HD	EPM	EFP
C_1		— Day of year —		d
	1	133.0	153.9	14.4
	2	135.0	153.7	15.7
	3	135.0	156.8	17.3
	4	135.0	149.8	11.8
	5	137.0	152.1	10.6
	6	140.5	156.0	12.0
	SE	3.5	3.4	3.8
C_2	1	130.0	147.5	11.6
	2	130.0	154.4	17.9
	3	131.0	153.1	15.1
	4	131.0	148.9	11.4
	5	135.0	152.7	14.7
	6	136.0	152.8	13.3
	SE	2.5	3.8	2.4

Table 3. Correlations between heading date (HD), kernel growth rate (KGR), effective filling period (EFP), and estimated date of physiological maturity (EPM) in four selection cycles of wheat Population 1 (above diagonal) and wheat Population 2 (below diagonal).

	HD	KGR	EFP	EPM
HD	-----	0.27**	−0.12	0.72**
KGR	0.45**	-----	−0.03	0.26**
EFP	−0.42**	−0.35**	-----	0.53**
EPM	0.84**	0.35**	0.05	-----

**Significantly different from zero at P<0.01. (Range in df was 29–63.)

Table 4. Narrow-sense heritability (h^2) estimates on a half-sib family-mean basis with 90% confidence intervals for traits in two wheat populations.

	Population 1			Population 2		
Trait†	h^2	Lower limit	Upper limit	h^2	Lower limit	Upper limit
HD	0.67**	0.29	0.88	0.81**	0.60	0.93
KGR	0.64**	0.22	0.87	0.69**	0.34	0.89
EFP	0.27‡	----	----	0.50*	−0.07	0.82
EPM	0.45*	−0.18	0.81	0.68**	0.31	0.89
Yield	0.10	----	----	0.62**	0.25	0.86

*,**Significantly different from zero at $P<0.10$, 0.05, respectively.
†HD = heading date, KGR = kernel growth rate, EFP = effective filling period, EPM = estimated date of physiological maturity.
‡Broad-sense estimate.

Table 5. Additive genetic correlations between heading date (HD), kernel growth rate (KGR), effective filling period (EFP), estimated date of physiological maturity (EPM), and yield in wheat Population 1 (above diagonal) and wheat Population 2 (below diagonal).

	HD	KGR	EFP	EPM	Yield
HD	----	0.58†	−0.51†‡	1.25†	2.75
KGR	−0.02	----	−0.70†‡	0.53†	0.13
EFP	−0.01	−0.43†	----	1.70†‡	§
EPM	0.94	−0.28†	0.39	----	1.24
Yield	−0.51	1.15	−0.70	−0.78	----

†Genetic covariance exceeds twice its standard error.
‡Correlation reflects nonadditive genetic variance and covariance.
§Additive genetic correlation not estimated.

additive genetic variance for traits related to maturity was reflected in moderate to high narrow-sense heritability estimates (Table 4). For example, the heritability of heading date was 0.67 ($P < 0.05$) in Population 1 and 0.81 ($P < 0.05$) in Population 2. These heritability estimates for heading date are intermediate in magnitude to those reported previously (Johnson et al., 1966; Schlehuber et al., 1967; Anwar and Chowdhury, 1969; Bhatt, 1972; Avey et al., 1982; Frederickson and Kronstad, 1985). It should be noted that our estimates may be inflated by genotype × location and genotype × year interactions. The magnitude of these estimates suggests that half-sib family selection conducted in the populations should produce changes in heading, date, KGR, and EPM in Population 1 and heading date, KGR, EFP, EPM, and yield in Population 2.

In Population 1, several additive genetic correlations (r_a) exceeded one (Table 5). The most likely explanation for these problematic estimates is that estimates of the additive genetic covariance were inflated by genotype × environment interaction. It is also possible that the Design I linear model did not fit the data, yielding spurious estimates of genetic variance and covariance. Alternatively, sampling error could account for correlations greater than one.

Given the problems in accurately estimating additive genetic correlations, it was difficult to obtain meaningful estimates of predicted correlated response to selection in Population 1. In Population 2, the sign and magnitude of the r_a and heritability estimates were generally favorable for the development of genotypes with early EPM (Table 5). The negative r_a between EPM and yield indicates that selection for early EPM would not reduce yield. Predicted direct response to one cycle of half-sib family selection for early EPM with a 10% selection intensity was −2.1 d. Predicted correlated response in EPM to one cycle of half-sib family selection for early heading date was −2.2 d. Thus, indirect selection predicts slightly more progress than direct selection. Furthermore, selection for early heading date would be preferred to selection for EPM because of the labor involved in estimating KGR, EFP, and EPM.

The question, then, is how to apply these findings to a wheat breeding program in which the objective is to develop earlier-maturing genotypes. In our study, heading date was not always highly correlated with time of physiological maturity. It is common practice to conduct single plant and family selection in early generations followed by yield testing beginning in the F_4 or F_5 generation. In early generations when it is necessary to screen a large number of genotypes and seed amounts preclude measurement of EPM, heading date should be used as an approximate maturity rating. In later generations, when seed supply is not limiting and fewer entries are tested, a maturity rating based on EPM would ensure continued selection pressure for early physiological maturity. Significant additive genetic variance for EPM detected in the Design I analysis suggest that normal selection schemes for self-pollinated crops should result in progress from selection.

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REFERENCES

Allard, R.W. and J. Harding. 1963. Early generation analysis and prediction of gain under selection in derivatives of a wheat hybrid. Crop Sci. 3:454–456.
Anwar, A.R., and A.R. Chowdhury. 1969. Heritability and inheritance of plant height, heading date, and grain yield in four spring wheat crosses. Crop Sci. 9:760–761.
Avey, D.P., H.W. Ohm, F.L. Patterson, and W.E. Nyquist. 1982. Three cycles of simple recurrent selection for early heading in winter wheat. Crop Sci. 22:908–912.
Bhatt, G.M. 1972. Inheritance of heading date, plant height and kernel weight in two spring wheat crosses. Crop Sci. 12:95–98.
Bruckner, P.L., and R.C. Frohberg. 1987. Rate and duration of grain fill in spring wheat. Crop Sci. 27:451–455.
Carmer, S.G., W.M. Walker, and R.D. Seif. 1969. Practical suggestions on pooling variances for F tests of treatment effects. Agron. J. 61:334–336.
Clarke, J.M. 1983. Time of physiological maturity and post-physiological maturity drying rates in wheat. Crop Sci. 23:1203–1205.
Comstock, R.E., and H.F. Robinson. 1948. The components of genetic variance in populations of biparental progenies and their

use in estimating the average degree of dominance. Biometrics 4:254–260.
Daynard, T.B., and W.G. Duncan. 1969. The black layer and grain maturity in corn. Crop Sci. 9:473–476.
Daynard, T.B., S.W. Tanner, and W.G. Duncan. 1971. Duration of the grain filling period and its relation to grain yield in corn, *Zea mays* L. Crop Sci. 11:45–48.
Eastin, J.D., J.H. Hultquist, and C.Y. Sullivan. 1973. Physiologic maturity in grain sorghum. Crop Sci. 13:175–178.
Egli, D.B. 1976. Planting date, row width, population, and growth regulators. p. 56–62. *In* L.D. Hall (ed.) World Soybean Research. Proc. World Soybean Res. Conf., Champaign, IL. 3–8 Aug. 1975. Interstate Publishers, Danville, IL.
Falconer, D.S. 1981. Introduction to quantitative genetics. 2nd ed. Longman, London.
Florell, V.H. 1924. Studies on the inheritance of earliness in wheat. J. Agric. Res. 29:333–347.
Frederickson, L.J., and W.E. Kronstad. 1985. A comparison of intermating and selfing following selection for heading date in two diverse winter wheat crosses. Crop Sci. 25:555–560.
Hanft, J.M., and R.D. Wyche. 1982. Visual indicators of physiological maturity in hard red spring wheat. Crop Sci. 22:584–588.
Harlan, H.V. 1923. Water content of barley kernels during growth and maturation. J. Agric. Res. 23:333–360.
Johnson, V.A., K.J. Biever, A. Haunhold, and J.W. Schmidt. 1966. Inheritance of plant height, yield of grain, and other plant and seed characteristics in a cross of hard red winter wheat. Crop Sci. 6:336–338.
Knapp, S.J., W.W. Stroup, and W.M. Ross. 1985. Exact confidence intervals for heritability on a progeny mean basis. Crop Sci. 25:192–194.
Large, E.C. 1954. Growth stages in cereals. Plant Pathol. 3:128–129.
May, L. 1990. Selection for early heading date and correlated response in traits related to maturity in winter wheat. Ph.D. diss. Univ. of Kentucky, Lexington. (Diss. Abstr. AAC9109298).
Mode, C.J., and H.F. Robinson. 1959. Pleiotropism and the genetic variance and covariance. Biometrics 15:518–537.
Nass, H.G., and B. Reiser. 1975. Grain filling period and grain yield relationships in spring wheat. Can. J. Plant Sci. 55:673–678.
Norman, A.G. 1978. Soybean physiology, agronomy, and utilization. Academic Press, New York.
Pinthus, M.J., and Y. Sar-Shalom. 1978. Dry matter accumulation in the grains of wheat (*Triticum aestivum* L.) cultivars differing in grain weight. Ann. Bot. 42:469–471.
Satterthwaite, F.E. 1946. An approximate distribution of estimates of variance components. Biometr. Bull. 2:110–114.
Saunders, C.E. 1928. The development of the wheat kernel. Sci. Agric. 8:524–531.
Schlehuber, A.M., D.C. Abbott, B.R. Jackson, and B.C. Curtis. 1967. Correlated inheritance of maturity and quality factors in a hard red winter wheat cross. Crop Sci. 7:13–16.
Shaw, R.H., and W.E. Loomis. 1950. Basis for the prediction of corn yields. Plant Physiol. 25:225–244.
Singh, V.P., M. Singh, and M.S. Kairon. 1984. Physiological maturity in *aestivum* wheat: Visual determination. J. Agric. Sci. 102:285–287.
Sofield, I., L.T. Evans, M.G. Cook, and I.F. Wardlaw. 1977. Factors influencing the rate and duration of grain filling in wheat. Aust. J. Plant Physiol. 4:785–797.
Van Sanford, D.A. 1985. Variation in kernel growth characters among soft red winter wheats. Crop Sci. 25:626–630.
Warrington, I.J., R.L. Dunstone, and L.M. Green. 1977. Temperature effects at three development stages on the yield of the wheat ear. Aust. J. Agric. Res. 28:11–27.
Weigand, C.L., and J.A. Cuellar. 1981. Duration of grain filling and kernel weight as affected by temperature. Crop Sci. 21:95–101.